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Characteristics of exotic ants in North America

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Abstract
The worldwide transport of species beyond their native range is an increasing problem, e.g. for global biodiversity. Many introduced species are able to establish in new environments and some even become invasive. However, we do not know which traits enable them to survive and reproduce in new environments. This study aims to identify the characteristics of exotic ants, and to quantitatively test previously postulated but insufficiently tested assumptions. We collected data on nine traits of 93 exotic ant species (42 of them being invasive) and 323 native ant species in North America. The dataset includes 2536 entries from over 300 different sources; data on worker head width were mostly measured ourselves. We analyzed the data with three complementary analyses: univariate and multivariate analyses of the raw data, and multivariate analyses of phylogenetically independent contrasts. These analyses revealed significant differences between the traits of native and exotic ant species. In the multivariate analyses, only one trait was consistently included in the best models, estimated with AIC_c values: colony size. Thus, of the nine investigated traits, the most important characteristic of exotic ants as compared to native ants appears to be their large colony size. Other traits are also important, however, indicating that native and exotic ants differ by a suite of traits.

Keywords
alien species, Formicidae, Hymenoptera, insects, invasions, invasives, North America, tramp ants

Introduction

Due to globalization, more and more species are being transported across the globe and introduced to regions where they did not occur before. Such species have taken step

1 of the invasion process (Kolar and Lodge 2001; Jeschke and Strayer 2005, 2006). Species that have also established one or more self-sustaining populations in the wild in their exotic range (step 2) are called exotic established species here. Those species that have additionally spread substantially from their point of introduction (step 3) are called exotic invasive species here. Although the term "invasive" is sometimes reserved for species with clear negative impacts, we are not restricting our definition of invasive species in this way. Certainly, however, many exotic invasive species do have devastating effects, e.g. on biodiversity or ecosystem services (Pimentel et al. 2005; Kettunen et al. 2009).

A central question of invasion biology has been which species with which characteristics are the ones that establish themselves and become invasive. What separates such species from those that have not established populations in exotic ranges? Most studies focusing on this question investigated plants and vertebrates (reviewed in Kolar and Lodge 2001; Jeschke and Strayer 2006; Richardson and Pyšek 2006), whereas only a few studies have looked at invertebrates (Mondor et al. 2007; Statzner et al. 2008; Šefrová and Laštůvka 2009). Here, we investigate this question for ants (Hymenoptera: Formicidae).

Most countries and regions of the world are now populated by numerous exotic ant species. Hawaii, for instance, has no native ants but 51 exotic established ant species (Starr et al. 2008). McGlynn (1999a) listed 147 ant species that have established themselves beyond their native range. Despite the existence of many invasive ants, most studies have focused on a few invasive ant species, e.g. the Argentine ant *Linepithema humile*, the big-headed ant *Pheidole megacephala*, or the red imported fire ant *Solenopsis invicta* (Holway et al. 2002). These species are also included in the Global Invasive Species Database's (2011) list of *100 of the World's Worst Invasive Alien Species*. As most studies on invasive ant species have focused on a few species, quantitative studies that compare many species have been largely lacking (but see McGlynn 1999b; Lester 2005; King and Porter 2007).

Despite this lack of formal quantitative analyses, exotic established and invasive ants are often assumed to have the following characteristics (Passera 1994; McGlynn 1999b; Holway et al. 2002; Tsutsui and Suarez 2003): their colonies have (1) more reproducing queens (polygyny) and (2) more workers than the colonies of native species; (3) they form new nests more frequently via budding than native species; and their workers are (4) more frequently monomorphic, (5) smaller, and (6) more frequently sterile than the workers of native or unsuccessfully introduced species. There are only few previous studies that quantitatively tested any of these six assumptions by comparing many ant species. With respect to assumption 5 that exotic ant species have smaller workers than native species, McGlynn (1999b) compared worker head width – a standard measure of body size in ants (Wilson 1980; Hölldobler and Wilson 1990; Kaspari 1993) – between 78 exotic and 233 native ants, finding that the workers of exotic ants are smaller than their native relatives. Lester (2005) similarly found for 66 species introduced to New Zealand that smaller species are better able to establish themselves than larger species. By contrast, King and Porter (2007) found no obvious

difference in body size between 94 native and 13 exotic ant species in Florida. Their results also do not support assumption 2 that exotic ant species form larger colonies than native species. In conclusion, quantitative tests of the six mentioned assumptions have been largely lacking, and the few tests that do exist had mixed results.

Using a dataset with more than 400 species, we quantitatively tested the six assumptions about the characteristics of exotic ants by comparing traits of exotic and native ant species in North America. These comparisons were done twice: once between exotic established ants and native ants, and once between exotic invasive ants and native ants. We expected that differences will be more pronounced for the latter comparison, as exotic invasive ants are the subset of exotic established ants that have successfully completed the full invasion process. If our analysis identifies traits that are related to the success of ant species in new environments, these traits should be more pronounced in the subset of invasive species.

Methods

Geographic Focus

We focused on regions that are particularly well investigated with respect to exotic ants: 14 states of the U.S. (Alabama, Arizona, Arkansas, California, Florida, Georgia, Illinois, Louisiana, Mississippi, Missouri, North Carolina, Ohio, South Carolina, and Tennessee) and one state of Mexico (Baja California). This study area has definite and naturally given borders (e.g. coastlines) and is part of the Nearctic and Neotropic bioregion, with mean annual temperatures from 10° C in northern Illinois and northern California, to 25° C in southern Baja California and southern Florida (Geodata 2011). The area includes not only a wide range of temperatures but also a diversity of biomes, thus covering a broad range of conditions.

Species List

Our species list is based on the database AntWeb (2009) which is hosted by the California Academy of Sciences and lists native as well as exotic ant species. We added further exotic species from literature sources (given in Appendix 1) and based on personal communications with other researchers (see Acknowledgements), giving a total of 416 ant species. The category Exo (exotic established ant species; n = 93 species) includes all species that were reported as exotic, introduced, alien, non-indigenous, or non-native in at least one of the above mentioned 15 states. Since the discovery and determination of an ant colony requires a certain amount of persistence of that colony, it seems likely that such exotic species have established at least one colony in the relevant state(s) and have thus completed the first two steps of the invasion process (see above). The category Inv (exotic invasive ant species; n = 42) is a sub-category of Exo and includes those

species of this category that were given as exotic, introduced, alien, non-indigenous, or non-native in at least two of the above mentioned 15 states. Due to their occurrence in at least two states, it seems likely that they have spread and have thus completed all three steps of the invasion process, even if this cannot be fully revealed. Ants can spread either by human transport over short to large distances (jump dispersal) or naturally over short distances by themselves. Given that 86% of the species in this category were reported as present in directly neighboring states, many of them have probably spread naturally. Independently of whether or not the species in this category really completed the full invasion process, most of them have been more successful in their exotic range than the other species in the category Exo which were only reported to be present in one state. We thus expect stronger differences between ants of this category Inv and native ants (Nat; n = 323 species) than between all exotic (category Exo) and native ants. Our complete species list is given in Appendix 2.

Traits

In a literature search until July 2009, we collected data on traits of the 416 ant species in our species list. The sources included scientific papers, books, websites, and personal communications with researchers (Appendix 1 and Acknowledgements). Synonyms and antiquated names of species were noticed. Tools for searching were Google, Google Scholar, Google Books, and the ISI Web of Science. The complete dataset with references for all data points is provided as Appendix 3. It includes 2536 data points from over 300 different sources; data on worker head width of 414 ant species were measured ourselves. The nine specific traits we analyzed are as follows:

A) Gyny – the degree of gyny, i.e. the number of reproductive queens (corresponding to assumption 1 mentioned in the Introduction; n = 226 species). We differentiated between obligate monogyny (only one functional queen; n = 103), obligate polygyny (two or more functional queens; n = 67), and facultative monogyny/polygyny (n = 56).

B) Colony size – the mean colony size, defined as the average number of workers in a colony (corresponding to assumption 2; n = 227). For exotic species, it is the average number of workers in colonies in both the native and exotic range. Since this trait only relates to the workers of each species, we excluded the two parasitic species *Pogonomyrmex colei* (Snelling) and *Anergatus atratulus* (Schenk) that do not have a worker caste.

C) Founding – how new nests are founded (n = 190), either by the queen alone (independent; n= 144), with the help of accompanying workers (dependent; n = 35), or a mix of these strategies (n = 11). The category "independent" includes claustral, semiclaustral, and pleometrotic founding strategies. The category "dependent" is applicable to species that found new nests via budding, splitting, sociotomy, or fission. This trait corresponds to assumption 3 in the Introduction, but to an extended version of this assumption, as only budding as a characteristic of exotic ants has been previously assumed and has thus been mentioned in the Introduction. We consequently extended assumption 3 to assumption 3a: Exotic ants form new nests more frequently

in a dependent way than native ants. With respect to forming new nests, we additionally included information on social parasitism in our dataset:

D) Parasitism (n = 225) – we differentiated between facultatively or obligately parasitic species (n = 35; e.g. optional slaveholders, dulotic ants, or inquilines) and non-parasitic species (n = 190). We assumed that parasites, which depend on their host species being present in the exotic range, are found less frequently among exotic than among native species (assumption 3b).

The remaining traits only concern the workers of each species. As for colony size, we again excluded the two species *Pogonomyrmex colei* and *Anergatus atratulus* that do not have a worker caste.

E) Morphs – the morphology of the workers (n = 386) with the following categories: monomorphic (n = 265), dimorphic (n = 44), or polymorphic (n = 77) worker caste. This trait corresponds to assumption 4 in the Introduction. For testing assumption 5 on worker body size, we used data on head width and total body length. For simplicity, no differentiation was made between monomorphic, dimorphic, and polymorphic ant species here.

F) HW (head width; n = 414) – since literature values were only available for less than half of the species in our dataset (HW1; n = 178), we measured head width for all species ourselves, using the software ImageJ (2009). These measurements (HW2; n = 414) were carried out with digital photographs, showing the frontal view of workers. Following Hölldobler and Wilson (1990), we measured maximum head width without the workers' eyes. We measured five individuals of each species (except where this was not possible due to lacking photos) and then calculated average head width. Photos were acquired from authoritative websites (AntWeb 2009; Discover Life 2009; Mississippi Entomological Museum 2009). As the data from the literature (HW1) were highly correlated with the data we measured ourselves (HW2) (r = 0.954; analysis performed for species where we had both HW1 and HW2; n = 178), we merged these two variables to HW, using the mean of HW1 and HW2 for species where both data were available.

G) TL (total body length) – an alternative measure of body size in ants is total body length (n = 313). We collected these data from the literature, thereby not discriminating between different methods to measure body length, as such information was often not provided.

H) Reproduction – the reproductive ability of workers (n = 179), discriminating workers that are sterile (n = 90; without ovarioles) from those that are potentially fertile (n = 89; able to produce males, trophic eggs, or are thelytoke, i.e. produce females). This trait corresponds to assumption 6.

I) Stinger (n = 388) – we discriminated workers with a functional stinger (n = 232) from those without a stinger or a rudimental or non-functional stinger (n = 156). This trait does not belong to an assumption mentioned in the Introduction. In fact, no clear assumption with respect to the frequency of a functional stinger in exotic as compared to native ant species can be found in the literature, possibly because two intuitively reasonable lines of thought lead to opposite expectations. On the one hand,

a functional stinger represents a weapon that might be beneficial to survive in an exotic environment, hence one could expect that workers of exotic ants are more frequently equipped with a stinger than those of native ants. On the other hand, the stinger is a phylogenetically primary trait that has been secondarily lost in many ant species of derived clades (Hölldobler and Wilson 1990), questioning the adaptive advantage of having a stinger under at least some environmental conditions. Analyzing our data on stinger presence may help assess which of these two conflicting lines of thought is more applicable to exotic ants in North America.

For all metric literature data (colony size, HW1, and TL), we adopted means reported in the literature for a given species. If no mean but only an interval was reported (minimal and maximal limits for di- or polymorphic species; colony sizes for different colony ages), we calculated the mean by averaging the minimal and maximal value of each interval. If data for a given trait and species were available from more than one source, we calculated the mean by averaging across sources.

Analyses

Comparisons were done between native (Nat) and exotic established (Exo) ants, and between native and exotic invasive (Inv) ants. We applied univariate analyses, multivariate analyses of the raw data, and multivariate analyses of phylogenetically corrected data. For the univariate analyses, we performed two different two-sample tests for each of our nine traits. In these tests, one sample consisted of Nat species; the other sample consisted of Exo species for the first test and of Inv species for the second test. In the multivariate analyses, the independent variables were the traits, and the dependent variable was the species category: Nat/Exo for the first comparison and Nat/Inv for the second comparison. In our analyses, we followed the approach taken by Jeschke and Strayer (2006, 2008) and Jeschke and Kokko (2008) to combine the strengths of univariate and multivariate analyses by performing both types of analysis and interpreting them jointly. Univariate analyses have the advantage that all species can be considered for which data on a certain trait are available. In multivariate analyses, however, only those species can be considered for which data on all traits are available. As our dataset includes empty cells, multivariate analyses will have a smaller sample size than univariate analyses. On the other hand, the species being lost in the multivariate analyses will be those that are not as well investigated as species for which data on all traits are available. The data on the latter species are thus probably more reliable, and some data of species additionally included in univariate analyses might not be reliable. An additional drawback of univariate analyses is that their results have to be interpreted with caution, as spurious correlations cannot be detected, and the relative importance of different variables for explaining observed variations cannot be inferred. The latter can only be achieved with multivariate analyses. As Jeschke and Strayer (2006, 2008) and Jeschke and Kokko (2008), we performed two types of multivariate analyses: one with the raw data and one with phylogenetically corrected data. Details of these three com-

plementary analyses – (A) univariate analyses of the raw data, (B) multivariate analyses of the raw data, and (C) multivariate analyses of phylogenetically independent contrasts – follow in the next paragraphs. Their complexity increases from A to C, while their sample size decreases. When interpreting the results, we consider all three analyses jointly. For the reasons given above, however, we put most weight on the multivariate analyses of phylogenetically independent contrasts. If not stated otherwise, statistical analyses were performed with PASW Statistics version 17.0.

A) For the univariate analyses, we ran two-tailed binomial tests for the binary variables parasitic, reproduction, and stinger; *U*-tests were done for the ordinal variables gyny, founding, and morphs; and *t*-tests for unequal variances were run for the metric variables HW, TL, and colony size.

B) As mentioned above, multivariate analyses can only consider those species for which data on all included variables are available. As our dataset includes empty cells, reducing the number of variables in the multivariate analysis increases the number of species in the analysis and thus the sample size. This is one reason why it is necessary to consider *a priori* knowledge and thoroughly think about which variables should be included in a multivariate analysis and which should be excluded; further reasons are given in Burnham and Anderson (2002). We excluded the variable TL (total body length), as it was available for fewer species than HW (head width), the other variable quantifying body size. We also excluded the variable parasitism from the multivariate analyses, as it was uninformative in the reduced dataset of the multivariate analyses: all species in the reduced dataset were non-parasitic. The remaining seven traits were included as independent variables in the multivariate analyses: gyny, colony size, founding, HW, morphs, reproduction, and stinger. The species list decreased to $n = 70$ for the comparison of native and exotic established ants, and to $n = 60$ for the comparison of native and exotic invasive ants. For all combinations of traits, but excluding interactions, we calculated multiple logistic regressions (due to our binary dependent variables: Nat, Exo, and Inv). For each of the two comparisons, we thus calculated $2^7 - 1 = 127$ regression models. We evaluated the models by means of AIC_c values (Akaike's information criterion corrected for small sample size, Burnham and Anderson 2002).

C) As our data quantify traits of species that are phylogenetically related to each other, they are not independent of each other. To correct for this phylogenetic dependence, we calculated phylogenetically independent contrasts (Felsenstein 1985; Garland et al. 1992, 1999, 2005; Pagel 1992), using Mesquite version 2.71 (Maddison and Maddison 2009) and the PDAP module version 1.14 (Midford et al. 2008). Branch lengths were set according to Pagel's (1992) method. The phylogeny was taken from the literature and is freely available from the authors upon request (sources are provided in Appendix 1). A drawback is that phylogenetic relationships among ant species are not fully resolved, which is one reason why the results of raw-data multivariate analyses should be considered as well. Another reason is that similarities and differences between both types of analyses are informative (Garland et al. 1999). Independent contrasts are not binary, so we ran linear regressions in this case that were forced through the origin, which is necessary when analyzing independent contrasts (Garland et al. 1992). The same traits and reduced datasets were used as for multivariate analyses of the raw data.

Results

The above mentioned existing assumptions on differences between exotic and native ant species are supported by the univariate analyses. As expected, ant species that are exotic in North America (Exo and Inv) are more often polygynous than native (Nat) species (assumption 1; Fig. 1a; for both comparisons, Nat vs. Exo and Nat vs. Inv, $p < 0.001$) and form new nests more frequently in a dependent way (assumption 3a; Fig. 1b; both $p < 0.001$). Social parasitism is infrequent among all ant species but especially rare among exotic established (3%) and invasive (0%) species (native species: 20%; assumption 3b; Fig. 1c; both $p < 0.001$). Workers of exotic ants are mostly monomorphic, whereas those of native species tend to be more polymorphic (assumption 4; Fig. 1d; $p < 0.001$ and $p < 0.05$, respectively). Furthermore, head widths of exotic established (mean = 0.725 mm; SE = 0.037) and invasive species (mean = 0.699 mm; SE = 0.050) are significantly smaller than those of native species (mean = 1.051 mm; SE = 0.032) (assumption 5; Fig. 2a; both $p < 0.001$). As expected, the differences for total body length (TL) are similar to those of head width: workers of exotic established (mean = 2.99 mm; SE = 0.17) and invasive species (mean = 2.81 mm; SE = 0.24) have significantly shorter bodies than those of native species (mean = 4.22 mm; SE = 0.13) (both $p < 0.001$). Sterility is more frequent among workers of exotic established (78%) and invasive (93%) species than among natives (40%) (assumption 6; Fig. 1e; both $p < 0.001$). Finally, colonies of exotic established (mean ≈ 123037; SE ≈ 63591) and invasive species (mean ≈ 136777; SE ≈ 87659) are larger than those of native species (mean ≈ 6265; SE ≈ 1688) (assumption 2; Fig. 2b), but differences are not significant here. Please note that colony size is highly variable, however, ranging from five individuals to millions of workers for the species analyzed here. Thus, all assumed trait differences (assumptions 1–6) are shown by the data and are significant in the univariate analyses except for colony size which is highly variable. Still, the trend shown by the data for colony size is in the assumed direction. Also as expected, differences between exotic and native species are usually more pronounced if only exotic invasive species are compared with the native species. With respect to the presence of a functional stinger, workers of exotic established (72%) and invasive (76%) ants are significantly more frequently equipped with a functional stinger than those of native species (56%) (Fig. 1f; both $p < 0.01$).

Only multivariate analyses can reveal the relative importance of traits to differentiate between exotic and native ant species. In the four types of multivariate analyses that we performed, the only variable that is included in all models with substantial empirical support (Akaike weight $\omega_i \geq 0.05$, Table 1) is colony size, suggesting that a large colony size is the most important characteristic of exotic ants as compared to native ants in North America. The mode of colony founding and the reproductive ability of workers also appear to be particularly important variables to differentiate between exotic and native ant species, as they are included in many models with substantial empirical support. The remaining variables seem less important.

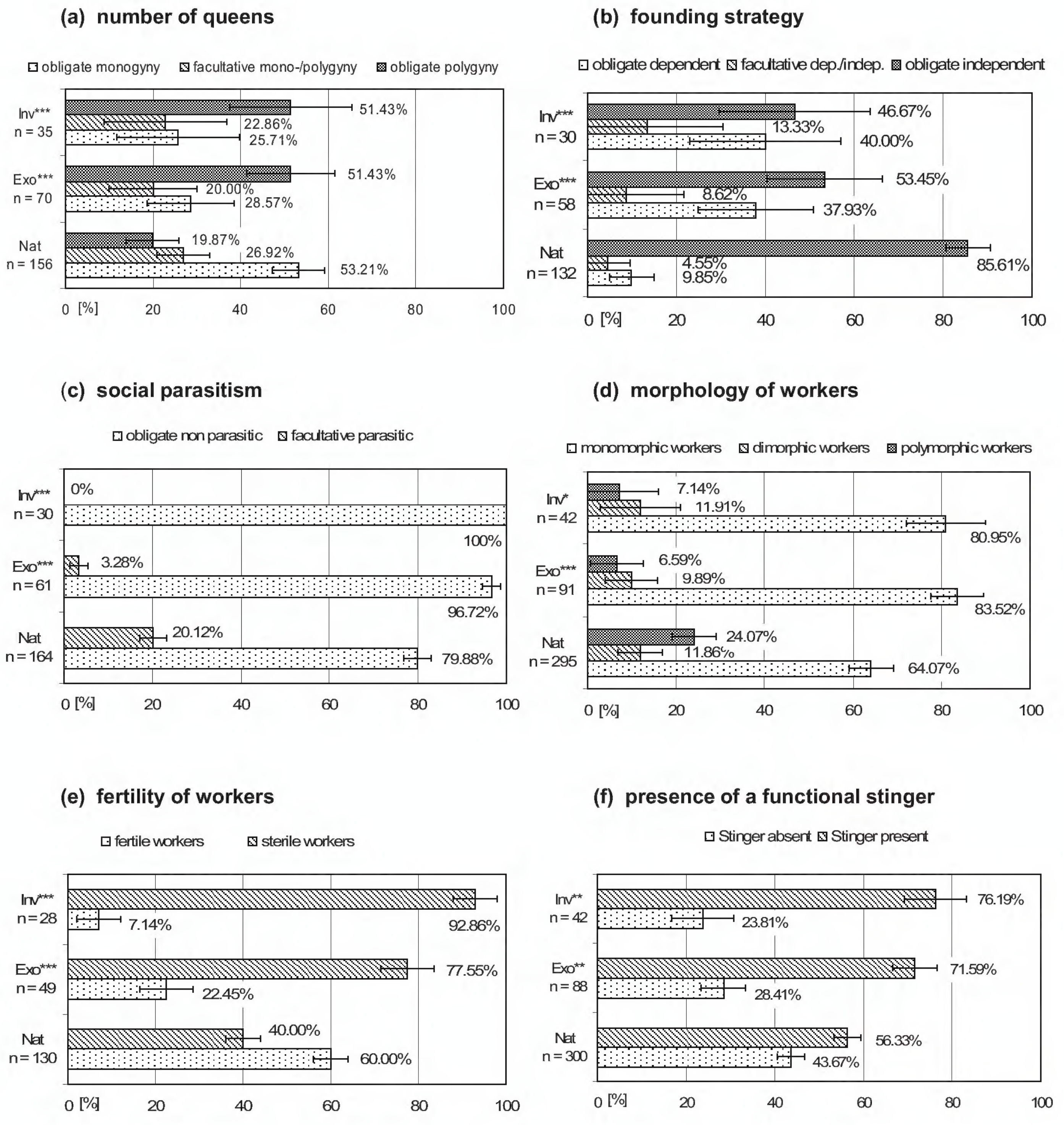

Figure 1. Results of univariate analyses, categorical traits. Differences among native (Nat), exotic established (Exo), and exotic invasive (Inv) ants in North America. Illustrated are means ± SE. Asterisks indicate significant differences between native and exotic established species, and between native and exotic invasive species: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Discussion

We examined traits of exotic and native ant species in North America in order to test previously postulated but insufficiently tested assumptions on the characteristics of exotic ant species. Our results support all investigated assumptions. Thus indeed, colonies of exotic ant species have more reproducing queens (polygyny; assumption 1) and more workers (assumption 2) than colonies of native species; they form new nests more frequently in a dependent way than native species (assumption 3a); parasites

Table 1. Results of multivariate analyses. Shown are multivariate regression models with substantial empirical support, i.e. with Akaike weights $\omega_i \geq 0.05$, calculated on the basis of Δ_i AIC_c values which are shown as well. Models with low empirical support, i.e. with Akaike weights $\omega_i < 0.05$, are not shown. Each regression model compared native ants with either exotic established or exotic invasive ants, as indicated. Model inputs were either raw data or phylogenetically independent contrasts, also as indicated. Each model included the given variables' main effects.

Model (variables included)	Δ_i AIC_c	ω_i
Exotic established ants, raw data		
Colony size, founding, reproduction, morphs	0	0.203
Colony size, founding, reproduction, morphs, gyny	0.267	0.178
Colony size, founding, reproduction, morphs, HW	0.686	0.144
Colony size, founding, reproduction, morphs, gyny, HW	1.879	0.079
Colony size, founding, reproduction, morphs, stinger	2.467	0.059
Colony size, founding, reproduction, morphs, gyny, stinger	2.568	0.056
Exotic established ants, independent contrasts		
Colony size, founding	0	0.089
Colony size, founding, reproduction	0.983	0.055
Colony size, founding, stinger	1.011	0.054
Exotic invasive ants, raw data		
Colony size, founding, reproduction, morphs, gyny	0	0.428
Colony size, founding, reproduction, morphs, gyny, stinger	1.268	0.227
Colony size, founding, reproduction, morphs, gyny, HW	2.350	0.132
Colony size, founding, reproduction, morphs, gyny, HW, stinger	3.752	0.066
Exotic invasive ants, independent contrasts		
Colony size, reproduction	0	0.202
Colony size, reproduction, HW	1.264	0.107
Colony size, reproduction, founding	1.762	0.084
Colony size, reproduction, morphs	2.267	0.065
Colony size, reproduction, gyny	2.295	0.064
Colony size, reproduction, stinger	2.300	0.064

are found less frequently among exotic than among native species (assumption 3b); and the workers of exotic species are more frequently monomorphic (assumption 4), smaller (assumption 5), and more frequently sterile than the workers of native species (assumption 6). As expected, differences between exotic invasive and native species are more pronounced and in the same direction than differences between exotic established and native species.

Of the six assumptions, only assumptions 2 and 5 were, to our knowledge, previously tested (see Introduction). Assumption 2, which says that exotic ant species tend to form larger colonies than native species, has been previously tested by King and Porter (2007) who had mixed results depending on the inclusion or exclusion of the red imported fire ant *Solenopsis invicta* in their analysis. Our results are based on a much larger dataset and support assumption 2.

Our results also support assumption 5, which says that the workers of exotic ant species are smaller than those of native species, and are in line with previous tests of this

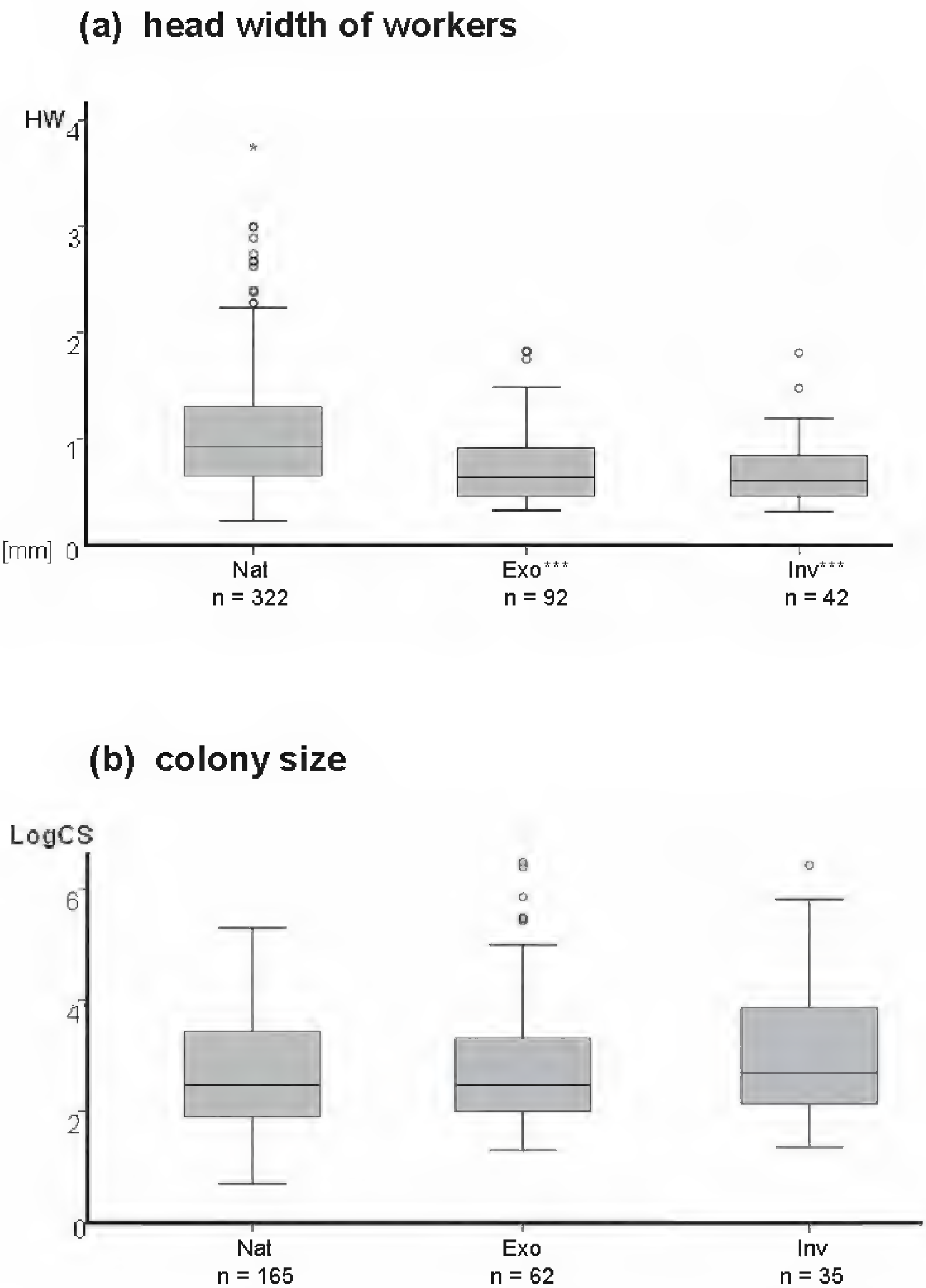

Figure 2. Results of univariate analyses, metric traits. Differences among native (Nat), exotic established (Exo), and exotic invasive (Inv) ants in North America. Asterisks indicate significant differences between native and exotic established species, and between native and exotic invasive species: $^{***}p < 0.001$ **a** Nat: median = 0.923 (range: 0.227 to 3.750), mean = 1.051 (SE = 0.032); Exo: median = 0.633 (range: 0.322 to 1.828), mean = 0.725 (SE = 0.037); Inv: median = 0.609 (range: 0.323 to 1.818), mean = 0.699 (SE = 0.050) **b** Nat: median = 296 (range: 5 to 200000), mean = 6265 (SE = 1688); Exo: median = 300 (range: 20 to 3000000), mean = 123037 (SE = 63591); Inv: median = 550 (range: 25 to 3000000), mean = 136777 (SE = 87659); differences between Nat and Exo (p = 0.071) and Nat and Inv (p= 0.146) were not significant here. Please note that the y-axis is $\log_{10}$-scaled here.

assumption by McGlynn (1999b) and Lester (2005), whereas King and Porter (2007) did not find an obvious difference in body size between exotic and native ant species. As mentioned above (Methods), we did not differentiate between monomorphic, dimorphic, and polymorphic ant species when measuring body size but simply used the average of five individuals. This approach was also used by King and Porter (2007), thus it cannot explain different results between their and our study. McGlynn (1999b) only used monomorphic species to avoid this problem. Using this approach for our dataset, thus restricting the analysis to monomorphic species, does not change our finding that workers of exotic ant species are typically smaller than workers of native ant species: Nat (n = 189): median = 0.781 (range: 0.227 to 2.380), mean = 0.829 (SE = 0.030); Exo (n = 76): median = 0.599 (range: 0.322 to 1.828), mean = 0.671 (SE = 0.039); Inv (n = 34): median = 0.564 (range: 0.323 to 1.818), mean = 0.653 (SE = 0.056). Both differences, between native and exotic species ($p < 0.01$) and between native and invasive species ($p < 0.01$), also remain significant for the restricted dataset. Another approach to correct body size for polymorphism was applied by Lester (2005) who measured the smallest and largest available ant for each species. Neither approach – taking the average of measured individuals, restricting the analysis to monophoric species, or measuring the smallest and larges available ant – is perfect, and this point demands further attention in future studies. Given currently available evidence, however, it seems that the workers of exotic ant species really are often smaller than the workers of native species.

Our results show that exotic ants have a suite of characteristics that separate them from the native ant fauna of North America (Table 2). The most important of these characteristics is, according to our multivariate analyses, colony size, followed by the founding strategy and reproductive ability of workers. Indeed, the univarate tests for differences in colony size were not significant, whereas the multivariate analyses identified this variable as the most important characteristic of exotic ants in North America. The non-significant results of the univariate analyses are less surprising when considering the huge variation in this trait, ranging from five individuals to several millions. Still, the trend shown by the univariate analyses was consistent with the multivariate analyses that exotic ant species have larger colonies than native species. Also, more weight should be put on the multivariate analyses, for the reasons given above in the Methods section. Within exotic species, there was a trend that exotic invasive species have larger colonies than exotic established species. It is reasonable that larger colonies have an advantage over smaller ones, especially when they are competing or even fighting with each other. A challenge with colony size is data availability: as the size of a colony depends on its stage (founding stage, ergonomic stage, or reproductive stage; Hölldobler and Wilson 1990), it would be desirable to compare colony size by correcting for colony stage. This was not possible for the current study due to lack of data. Another question is whether colony size of exotic species should be measured only in the native range, only in the exotic range, or in both ranges. We decided to take the average colony size in both ranges, as this measure best represents a species' overall average colony size. Other approaches are possible as well, but any approach currently suffers from the shortage of data on colony size. Once more data are available, it should be tested if colony size remains the most important characteristic of exotic ants.

Table 2. Summary of the combined results. Listed is the suite of traits that characterize exotic as compared to native ants, based on this study's results.

Characteristics of exotic ants
Large colony size
New nests founded by queen with workers[†] rather than queen alone
Not socially parasitic on other ants
Sterile workers
Monomorphic workers
More than one queen per colony (polygyny)
Small body size
Equipped with a functional stinger

[†]Dependent nest founding, either via budding, splitting, sociotomy, or fission.

In addition to colony size, the sterility of workers is an important characteristic of exotic ant species in North America, which is in line with the literature (Passera 1994; Holway et al. 2002). Species with large colonies consisting of sterile workers have a high probability to spread and thus to become invasive. Sterile workers do not invest their resources and those of their colony in their own reproduction, hence reproductive rivalries with the queen(s) or other workers are avoided (e.g. worker policing). Besides a large colony size and worker sterility, our results also show that exotic ants form new nests more frequently in a dependent way than native species, either via budding, splitting, sociotomy, or fission. Such a nest-founding strategy reduces the risk of the queen to die of starvation or predation. The queen can dedicate her resources to reproduction while the accompanying workers take care of foraging, defense, brood care, and other tasks.

Besides testing previously postulated assumptions, we also investigated if workers of exotic ant species differ from those of native ant species in the presence of a functional stinger. Our analyses revealed such a difference, showing that workers of exotic ant species are more frequently equipped with a functional stinger than workers of native ant species. Within exotic species, a functional stinger is more frequent in exotic invasive than exotic established species. These findings support the line of thought mentioned above that a functional stinger is a weapon that helps to survive in an exotic environment. Our dataset also showed a significant relationship of stinger presence with worker body size: workers of species with a functional stinger are smaller (mean head width in mm = 0.788, SE = 0.026, n = 232) than those of species without a functional stinger (mean = 1.259, SE = 0.052, n = 156) ($p < 0.001$, two-tailed t-test for unequal variances). Thus, species with large workers appear to often have lost their stinger in the course of evolution, probably because their large size is sufficient to be competitive. In species with small workers, on the other hand, the stinger may at least partly compensate for the size disadvantage.

A weakness of our dataset is that it does not include information on ant species that were introduced to North America but did not establish there. Even although sub-samples of ant species introduced to North America exist (Suarez et al. 2005), it is impossible to know all ant species that were introduced to North America and all that were not. We can, however, speculate to which extend observed differences between ex-

otic and native ant species are influenced by an introduction bias (Blackburn and Duncan 2001; Cassey et al. 2004; Jeschke and Strayer 2006; Blackburn and Jeschke 2009; van Kleunen et al. 2010). An introduction bias with respect to body size seems likely: Introductions of ants and other invertebrates are typically unintentional (Hulme et al. 2008), and since it is easier for small organisms than for large ones to remain undetected by the human eye, small ant species are probably more frequently introduced to North America than large species (see Mondor et al. (2007) and Šefrová and Laštůvka (2009) for similar arguments on aphids and lepidopterans, respectively). It is thus possible that observed differences between exotic and native ant species in body size are at least partly attributable to an introduction bias. There might be introduction biases with respect to other investigated traits as well, but they are less obvious and possibly less pronounced.

Another weakness of this study is that it can only provide correlative patterns rather than causative findings. For example, our finding that exotic ants have larger colonies than native ants does not necessarily imply that they successfully established *because* they form larger colonies. Despite limitations of this study, it may nonetheless contribute to a better understanding of exotic ant species. Together with a few other studies, this study also sheds light on differences between native and exotic invertebrates. Combining these differences with those found for vertebrates and plants will substantially improve our understanding of the general characteristics of exotic as compared to native species.

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Appendix 1

Literature sources. (doi: 10.3897/neobiota.10.1047.app1) File format: PDF.

Explanation note: This file lists all literature sources for our dataset, phylogeny, and species list.

Citation: Wittenborn D, Jeschke JM (2011) Characteristics of exotic ants in North America. NeoBiota 10: 47–64. doi: 10.3897/neobiota.10.1047.app1

Appendix 2

Species list. (doi: 10.3897/neobiota.10.1047.app2) File format: PDF.

Explanation note: This file lists all species included in our analyses. The species are subdivided into native, exotic established, and exotic invasive ant species.

Citation: Wittenborn D, Jeschke JM (2011) Characteristics of exotic ants in North America. NeoBiota 10: 47–64. doi: 10.3897/neobiota.10.1047.app2

Appendix 3

Dataset. (doi: 10.3897/neobiota.10.1047.app3) File format: Excel spreadsheet (xls).

Explanation note: This file provides our complete dataset with references for all data points.

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Citation: Wittenborn D, Jeschke JM (2011) Characteristics of exotic ants in North America. NeoBiota 10: 47–64. doi: 10.3897/neobiota.10.1047.app3